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**Fiddler crabs impact the structure of the benthic
macroinvertebrate community and the spatial distribution of
foraging shorebirds in tropical intertidal mudflats**

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Resumo Alargado

Os engenheiros de ecossistemas são organismos que transformam ou criam habitats, afetando muitas outras espécies. Os ecossistemas intertidais estão entre os mais produtivos do planeta e têm um papel vital na sobrevivência de muitos vertebrados, nomeadamente peixes e aves. A sua importância é especialmente relevante para aves costeiras migradoras fora da época de reprodução uma vez que várias espécies apenas se alimentam de macroinvertebrados bentónicos presentes nestas áreas. O caranguejo-violinista, *Afruca tangeri*, é descrito como um engenheiro de ecossistemas em bancos de vasa intertidais, onde tem impactes importantes, nomeadamente na alteração das características biogeoquímicas do sedimento e do ciclo de nutrientes. Além destes impactes, o caranguejo-violinista integra a dieta de grande parte das aves costeiras presentes no seu habitat, o que o torna um recurso muito importante.

Este estudo visou investigar a influência que as populações de caranguejo-violinista têm na estrutura da restante comunidade de macroinvertebrados bentónicos e dos seus principais predadores, as aves costeiras, no arquipélago dos Bijagós, Guiné-Bissau. O estudo decorreu em Adonga, no Parque Nacional de Orango, no arquipélago dos Bijagós. Para cumprir os objetivos foram selecionados dois tipos de área: com elevada e com baixa densidade de caranguejos. Em ambos os tipos de áreas, procedeu-se à amostragem da comunidade de macroinvertebrados bentónicos utilizando *cores* de sedimento. Posteriormente todos os invertebrados recolhidos foram identificados ao nível taxonómico mais baixo possível e, para cada tipo de área, foi determinada a diversidade e riqueza da comunidade assim como a densidade, biomassa total e biomassa disponível para as aves (5 cm superficiais do sedimento) de cada *taxon* identificado. Foi também realizada uma amostragem da comunidade de aves costeiras recorrendo a parcelas marcadas em ambos os tipos de área analisadas e procedendo a contagens (intervaladas de uma hora) no período de 2h antes a 2h depois do pico da maré vazia. Posteriormente, para cada tipo de área, foi calculada a riqueza e diversidade da comunidade de aves costeiras e a densidade de cada uma das espécies de aves costeiras contadas. Foram ainda descritos e comparados o comportamento alimentar e a dieta de quatro espécies de aves: Maçarico-galego (*Numenius phaeopus*), Tarambola-cinzenta (*Pluvialis squatarola*), Perna-vermelha-comum (*Tringa totanus*) e Borrelho-grande-de-coleira (*Charadrius hiaticula*) com base em vídeos (3-4 mins) de indivíduos em alimentação. Com o objetivo de caracterizar as populações de caranguejo-violinista em cada tipo de área foram efetuados vídeos em 60 quadrados de amostragem. Posteriormente, os vídeos foram analisados e para cada tipo de área determinou-se a densidade, rácio sexual e distribuição das classes de tamanho das populações de caranguejo e ainda o rácio caranguejo/tocas nas áreas de elevada densidade de caranguejos. Por fim caracterizámos os dois tipos de área em termos de granulometria (percentagem de finos) e conteúdo de matéria orgânica do sedimento.

Áreas com elevada densidade de caranguejos demonstraram um maior conteúdo em finos e matéria orgânica no sedimento. Nestas mesmas áreas, as comunidades de aves costeiras e macroinvertebrados apresentaram menor riqueza, diversidade e densidade, e, no caso dos macroinvertebrados, menor biomassa total e biomassa disponível para as aves. A comunidade de macroinvertebrados bentónicos em áreas com baixa densidade de caranguejo é dominada pelos poliquetas sedentárias das famílias Cirratulidae, Maldanidae e Capitellidae e pelos bivalves das famílias Veneridae (maioritariamente *Pelecypora isocardia*) e Lucinidae. Nas áreas com elevada densidade de caranguejo, as espécies acima referidas encontram-se também entre as mais abundantes, sendo ainda de mencionar os poliquetas errantes da família Nereidae e a substituição dos bivalves Lucinidae pela família Solecurtidae (maioritariamente *Tagelus adansonii*) como segundo bivalve mais abundante. É ainda de notar que os caranguejos-violinista tornam-se um dos *taxa* mais abundantes em áreas com elevada densidade de caranguejo, ultrapassados apenas pelo bivalve *P. isocardia*. Não obstante, os caranguejos-violinistas são, isoladamente e com uma margem muito significativa, o *taxon* com os

maiores valores de biomassa nestas áreas. Foram encontrados ainda 13 taxa em áreas com baixa densidade de caranguejo que estão completamente ausentes em áreas com elevada densidade de caranguejo.

A comunidade de aves costeiras em áreas com elevada densidade de caranguejos é caracterizada pela dominância de Maçarico-galego (*Numenius phaeopus*), Perna-vermelha-comum (*Tringa totanus*), Maçarico-das-rochas (*Actitis hypoleucos*) e Íbis-sagrada (*Treskiornis aethiopicus*), sendo que o Maçarico-das-rochas ocorre quase exclusivamente nestas áreas. Todas estas espécies consomem preferencialmente caranguejos-violinista. Em contraste, em áreas com baixa densidade de caranguejos, a comunidade de aves costeiras é dominada por Pilrito-de-bico-comprido (*Calidris ferruginea*), Seixoeira (*Calidris canutus*), Borrelho-grande-de-coleira (*Charadrius hiaticula*), Pilrito-das-praias (*Calidris alba*), Pilrito-de-peito-preto (*Calidris alpina*) e Pilrito-pequeno (*Calidris minuta*), sendo este último quase exclusivo destas áreas. Todas estas espécies predam principalmente poliquetas, bivalves e/ou gastrópodes. As restantes espécies não demonstraram diferenças significativas na densidade entre áreas, sendo elas Fuselo (*Limosa lapponica*), Ostraceiro (*Haematopus ostralegus*), Tarambola-cinzenta (*Pluvialis squatarola*), Borrelho-de-testa-branca (*Charadrius marginatus*), Perna-verde (*Tringa nebularia*) e Rola-do-mar (*Arenaria interpres*). À exceção da Tarambola-cinzenta, todas as aves em alimentação nas áreas com baixa densidade de caranguejos apresentaram uma maior taxa de bicadas, mas essa diferença não se traduziu num maior sucesso alimentar. Praticamente não foram encontradas diferenças na dieta das aves entre áreas, à exceção de um maior consumo de bivalves/gastrópodes em áreas com baixa densidade de caranguejos por parte do Maçarico-galego e um maior consumo de bivalves/gastrópodes em áreas com elevada densidade de caranguejo por parte da Tarambola-cinzenta. Houve, no entanto, uma grande proporção de presas não identificadas devido ao seu pequeno tamanho e à distância a que os vídeos foram filmados.

Nas áreas com elevada densidade, as populações de caranguejo-violinista são constituídas por indivíduos de classes de tamanho maiores, sendo que caranguejos com uma largura de carapaça superior a 1 cm são quase exclusivos destas áreas. Encontrámos ainda um rácio sexual enviesado para o número de fêmeas nestas áreas e um dos menores rácios caranguejo/toca alguma vez descrito. Não encontrámos diferenças significativas de tamanho entre machos e fêmeas de caranguejo-violinista.

Este estudo destaca os possíveis efeitos das populações de caranguejo-violinista no seu habitat, particularmente mostra a existência de grandes diferenças na composição da comunidade de macroinvertebrados bentónicos e aves costeiras entre áreas com baixa e elevada densidade de caranguejos. Com o conhecimento adquirido após a realização deste estudo é possível prever a estrutura mais provável da comunidade de aves costeiras presentes numa área do arquipélago dos Bijagós com base apenas na presença de caranguejo-violinista e, daí, prever qual a importância dessas áreas para cada espécie de ave costeira presente. Apesar de uma grande proporção de espécies de aves costeiras incluir caranguejo-violinista na sua dieta, a maioria das espécies tende a evitar as áreas com elevadas densidades de caranguejos. A presença de caranguejos-violinistas e o seu impacto nos macroinvertebrados e nas aves podem, portanto, ser muito relevantes numa perspetiva conservacionista já que esta espécie de caranguejo está amplamente distribuída nos Bijagós, a segunda área mais importante para aves costeiras invernantes na África Ocidental.

Palavras-chave: *Afruca tangeri*, áreas intertidais, aves costeiras, engenheiros de ecossistemas, Guiné-Bissau.

Abstract

Ecosystem engineers are organisms able to transform or create habitats, indirectly affecting many other species. Fiddler crabs *Afruca tangeri* (Eydoux, 1835), have been described as ecosystem engineers of intertidal mudflats, delivering important impacts, namely by changing sediment biogeochemical characteristics and nutrient cycling. This study aimed to investigate the influence of the fiddler crab populations in the structure of the remaining benthic macroinvertebrate communities as well as on the spatial distribution of their main predators, i.e. shorebirds, in the Bijagós archipelago, Guinea-Bissau. To achieve this, we selected areas with high densities of fiddler crabs and areas with low density/absence of crabs and compared the diversity and density of macroinvertebrates and shorebirds between these areas. In addition, we described foraging behavior of four shorebird species in both types of areas. Study areas were further characterized by determining the granulometry and organic matter content of the sediment. Areas with high crab density were characterized by finer sediments and higher organic matter content. Both the macroinvertebrate and shorebird communities presented significantly lower diversity and densities in areas showing high crab density. Except for the Grey plover, all birds foraging in areas with low crab densities showed higher pecking rates, although we found no differences in the overall feeding success. This study highlights the diverse effects of fiddler crab populations on their habitat, in particular by modifying the composition of the benthic macroinvertebrate fauna and associated shorebird communities. Although fiddler crabs are known to be an important prey item for many shorebird species, overall, high crab density areas are avoided by the majority of species within the shorebird community. Results from this study may be extremely relevant from a conservation perspective as fiddler crabs are widespread in the intertidal mudflats of the Bijagós archipelago, the second most important area for wintering shorebirds in West Africa.

Key-words: *Afruca tangeri*, ecosystem engineers, Guinea-Bissau, intertidal mudflats, shorebirds

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Introduction

Keystone species are “species that maintain the organization, stability and function of their communities, and have disproportionately large, inimitable impacts on their ecosystems by performing essential ecological functions” (Hale & Koprowski, 2018). This concept was first introduced in 1996 by Paine (1996) to explain the large top-down influence that purple sea stars (*Pisaster ochraceus*) and sea snails (*Charonia* spp.) have on their respective communities by performing their role as predators. Since then, the concept evolved and now includes a great diversity of species and trophic levels, not only referring to species that have a direct impact on others but also to species whose influence transforms or creates habitats, thus affecting many other species indirectly (Ciechanowski et al., 2011; Law et al., 2014). These species are called ecosystem engineers, and are generally defined as species that create, alter, or maintain habitats, and influence community composition through non-trophic interactions (Jones et al., 1994). Ecosystem engineers can have a critical impact on population dynamics, community composition and ecosystem function (Kleinhesselink et al., 2014; Wright & Jones, 2006). For example, the presence of the cushion plant *Azorella montantha* increases soil moisture and buffers temperature extremes which leads to an increase in species richness, thus altering species composition at a landscape-level (Badano et al., 2006). Prairie dogs are another example of ecosystem engineer as their constant grazing reduces vegetation volume and the cover of grasses and tall shrubs, increasing bare ground and forb cover, and creating and maintaining a whole new landscape (Baker et al., 2013).

Estuaries and other intertidal systems are among the world’s most productive ecosystems, maintaining complex trophic webs (Schelske & Odum, 1962; Day Jr et al., 2013). This high productivity is the key for the relevance of these areas for many vertebrate species including birds and fishes (Wallace et al., 1984; Burger et al., 1997). Intertidal mudflats are especially important for shorebird populations during migratory and non-breeding periods, as many species feed almost exclusively on benthic macroinvertebrates at low tide in this habitat (Quammen, 1984; Evans, 1999).

Several ecosystem engineer species inhabit intertidal mudflats, delivering important impacts in the whole system. Some plant species, such as the cordgrass *Spartina anglica* and the seagrass *Zostera noltii* reduce the hydrodynamic energy of the waves and currents, facilitating the establishment of other plant species (Bouma et al., 2005). Another cordgrass, *Spartina foliosa*, provides structure, oxygenates the sediment through its rhizomes (Josselyn, 1983), and maintains marsh elevation by trapping sediment (Cahoon et al., 1996). Animals, such as crabs, can also have a major role modifying this habitat, especially in tropical environments (Mouton & Felder, 1996; Botto & Iribarne, 2000; Kristensen, 2008). The burrowing activity of fiddler crabs (*Uca* spp., *Afruca* sp. and *Leptuca* spp.) is known to increase carbon flow, change the topography and biogeochemistry of the sediment and increase decomposition efficiency (Genoni, 1991; Mouton & Felder, 1996; Botto & Iribarne, 2000; Kristensen, 2008). These effects are the consequence of bioturbation, which is the forced ascension of deep organic matter and sediment to the surface, promoting growth and activity of bacteria (Katz, 1980; Montague, 1980a, b; Bertness, 1985; Gutiérrez et al., 2006; Kristensen, 2008).

Fiddler crabs are an abundant food source for shorebirds in many tropical mudflats during the non-breeding period (Boschi, 1964; Summers, 1980; Zwarts, 1985; Iribarne & Martinez, 1999; Lourenço et al. 2017). The easy access to this prey item leads many shorebirds to include it in their diet. For example, in Bahia Somborombon, in Argentina, waders are known predators of the fiddler crab *Uca uruguayensis* (Iribarne, 1999). In Guinea-Bissau, the majority of the shorebird species feeds on the fiddler crab *Afruca tangeri* and even some birds usually associated with pelagic and terrestrial food sources like the Common gull-billed tern (*Gelochelidon nilotica*) and the Palm-nut vulture (*Gypohierax angolensis*), respectively, resort to these crabs as prey (Zwarts, 1985). Some species, like the Whimbrel

(*Numenius phaeopus*) are true fiddler crab specialists, as can feed almost exclusively on crabs (Lourenço et al., 2017).

In addition of being an important prey item for shorebirds, the key role fiddler crabs play as ecosystem engineers, namely changing sediment biogeochemical characteristics and nutrient cycling, can potentially impact the benthic macroinvertebrate community, and thus indirectly impact their main predators, i.e., shorebirds (Mouton & Felder, 1996; Botto & Iribarne, 2000; Kristensen, 2008). To the best of our knowledge, the effects of fiddler crabs on other benthic macroinvertebrates have never been studied in detail, although the presence of these crabs has been shown to promote a decrease in meiofauna density, either by direct effects, such as predation, or by indirect effects, such as competition for food (Hoffman et al., 1984; Reinsel, 2004; Weis & Weis, 2004). Such effects may also hold true for macroinvertebrate communities. Moreover, bioturbation promoted by some crustaceans has been shown to have negative effects on mobile benthos, like errant polychaetes (Wilson, 1981; Jensen, 1985; Levinton, 1985; Tamaki, 1988) and sessile benthos (Stevens, 1928; Dorsey & Synnot, 1980; Posey, 1986; Pillay et al., 2007), like sedentary polychaetes, bivalves and gastropods, but these studies focused mainly on crayfish bioturbation and no study has been performed regarding the possible effects of the fiddler crabs' bioturbation.

The presence and density of fiddler crabs are likely not the only factors affecting macroinvertebrate and shorebird communities. Population characteristics such as size-class distribution and sex-ratio may be also important to explain the abovementioned effects. Larger crabs dig deeper and wider borrows (Lim & Diong, 2003), meaning that larger individuals will increase the sediment/air interface and the potential for biological and chemical reactions (Kristensen, 2008). Also, different shorebird species prey preferentially upon particular crab size classes, while avoiding others. Indeed, the size (maximum carapace width) of preyed crabs is highly correlated with the width of bird's bill and with its ability to break the crabs into small pieces (Zwarts, 1985). The marked sexual dimorphism exhibited by fiddler crabs, with adult males being larger than females, also leads to differences in burrow size between sexes (Lim & Diong, 2003). Also, fiddler crabs have sexually dimorphic claws: the males have one claw much larger than the other, while females have two similar (minor) claws. Whilst this characteristic makes males more threatening, leading some bird species to avoid preying on them (Bildstein, 1989), the claw increases male conspicuity making them potentially more attractive for birds that hunt with air strikes (Koga et al., 2001).

The fiddler crab *Afruca tangeri* (Eydoux, 1835) is widespread in the extensive intertidal mudflats of the Bijagós archipelago (Zwarts, 1985; Lourenço et al., 2017). This archipelago lies off the coast of Guinea-Bissau (11°12'N, 15°53'W) and comprises 88 islands and islets. The intertidal areas cover over 140,000 ha and are mostly dominated by large areas of soft sediment beds interspaced with smaller areas of sandy sediments, often bordered by mangrove trees (Pennober, 1999; Campredon & Catry, 2017). This archipelago is one of the world's most important wintering areas for shorebirds holding ca. 10% (ca. 700,000) of all birds that migrate along the East Atlantic Flyway (EAF; Salvig et al., 1994; Delany et al., 2009). Although the importance of this site is undisputed, many aspects of the ecology of shorebirds and their relationships with other key organisms are still poorly understood. In particular, only two studies have focused on the relationship between fiddler crabs and shorebirds in the Bijagós (Zwarts, 1985; Lourenço et al., 2017), both exclusively aiming to describe trophic relationships.

In this study we aim to understand the influence of fiddler crab populations in shaping the structure of the remaining benthic macroinvertebrate community as well as the spatial distribution of foraging shorebirds in the mudflats of the Bijagós archipelago. To fulfill this goal, we compared the density and species composition of the bird and infaunal communities among areas with low (control)

and high density of fiddler crabs. We further performed a characterization of these areas regarding relevant factors for macroinvertebrates such as sediment type (granulometry) and organic matter content. Also, we estimated if the foraging behavior and consumption of crabs by shorebirds varies among areas with different densities of fiddler crabs by analyzing video recordings of foraging birds. We predicted that areas with fiddler crabs have overall lower shorebird species richness and lower densities of shorebirds that feed on other macroinvertebrates but a higher density and species richness of shorebirds that preferably eat crabs.

Methods

Study area

The Bijagós archipelago (11°12'N, 15°53'W) arises from the continental shelf off Guinea-Bissau, near the mainland coast. It is an active deltaic archipelago, the only one on the Western coast of Africa (Pennober 1999). The archipelago and its intertidal flats and channels, covering an area of roughly one million hectares, possesses an astonishing biodiversity, which as lead to its classification as a Biosphere Reserve (1996) by UNESCO and as a Ramsar Site (2014) and has justified the creation of three marine protected areas and two National Parks. The large and complex network of channels that separates the 88 islands and islets of the archipelago is usually surrounded by mangroves and large mud and sand flats, which represent the largest extension of intertidal areas in Africa. This archipelago has a population of about 30,000 people and the inhabitants are predominantly farmers and fishermen (Thorne et al., 2013). The natural resources have been managed traditionally by the diverse Bijagós ethnic groups based on strong cultural and religious values (Henry, 1994). This has allowed a long-term conservation of the islands, for example by the active protection of sacred islands and islets and sacred forest patches where initiation rites take place, and which remain nearly untouched. This site is of crucial importance for many vertebrates, holding a total of 175 species of fish (Campredon & Catry, 2016), 17 species of reptiles (Catry et al., 2009; Aulyia et al., 2012), 282 species of bird (Dodman et al, 2004) and 29 species of mammal (Campredon & Catry, 2016). Moreover, the tidal flats and the mangroves of the archipelago play a major role in sustaining the productivity of fisheries resources, which has considerable weight in the national economy.

The present study took place in the intertidal flats near Adonga islet, part of the Orango National Park, in the Bijagós archipelago, Guinea-Bissau (Fig. 1) between February and April 2019. This is an uninhabited area, approximately 11 km long and possesses large extensions of intertidal mudflats bordered by mangroves. The mudflats have heterogeneous sandy and muddy patches cropped by a channel network around. Fiddler crabs occupy large extensions of these flats.

Fiddler crab distribution is a discreet phenomenon, rather than a continuum one, so there were no medium crab density areas as they were either present or absent from an area. The two classes analyzed were distinguished on the field based on the clear visual heterogeneity presented by the crab populations distribution and associated reworked sediment. Based on visual analysis, high crab density areas presented a greater abundance of crabs and strong signs of bioturbation, namely the crab burrows and revolved sediment while low crab density areas did not present either bioturbated sediment nor big crabs visible to the naked eye, although some very small crabs where present. The whole intertidal classification in low and high crab density presented in Fig. 1 was obtained by Belo (2019) using remote sensing techniques.

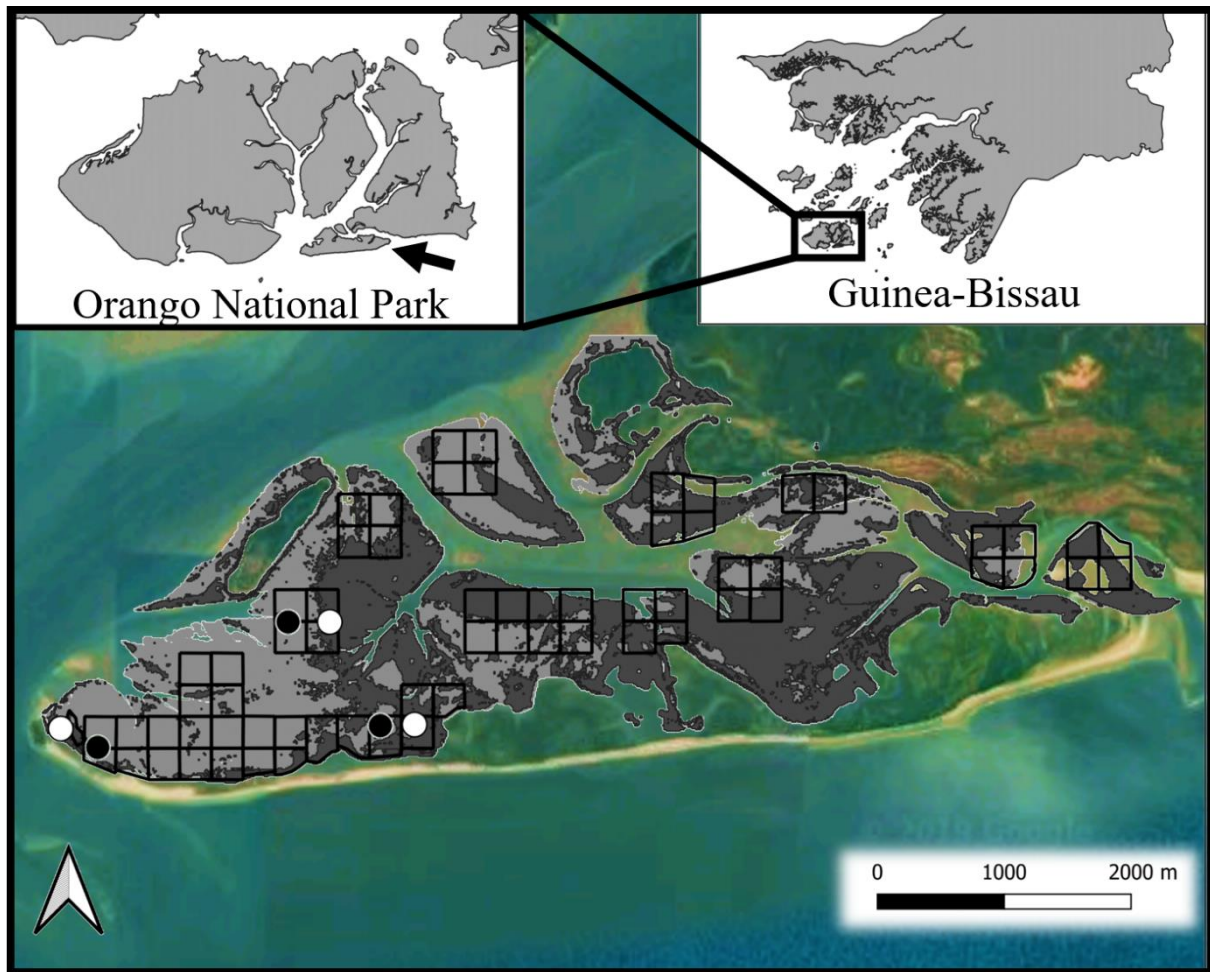


Fig. 1. Study area showing the intertidal mudflats around Adonga islet. Low and high crab density areas are represented by light and dark grey, respectively. Black squares represent the plots used for shorebird counts (each square roughly 250×250m). Circles show the sites selected for macroinvertebrate sampling, sediment sampling and crab video recordings: white circles with black outline – high crab density areas; black circles with white outline – low crab density areas. The black diagonal arrow shows the positioning of the Adonga islet within the Bijagós archipelago.

Macroinvertebrate collection and processing

Three areas of low and three of high crab density were selected to describe and compare macroinvertebrate communities (Fig. 1). Fifteen sediment cores (86.6 cm², approximately 20 cm deep) were collected in each area, totalizing 90 cores, 45 per crab density area. This sampling covered an area of about 625,000 m². Since most small macroinvertebrates inhabit the upper layers of the sediment, the top 5 cm of collected sediment were sieved in saltwater through a 0.5 mm mesh sieve and the deepest 15 cm of the core content were sieved using a 1 mm mesh. All invertebrates were immediately stored in 96% alcohol until further analysis.

In the laboratory all invertebrates were identified to the lowest possible taxonomic level using guides for eastern Atlantic polychaetes (Fauchald, 1977), bivalves, gastropods (Carpenter & Angelis, 2016) and crustaceans (Carpenter & Angelis, 2014). Afterwards, to determine biomass (measured as mg of ash-free dry weight, AFDW), each individual was dried to constant weight (at 60°C, during 48h) and

then incinerated in a muffle furnace (580°C, 2h). The samples were weighed after drying and again after incineration, and the biomass was calculated as the difference between dry weight and ash weight. We further determined the harvestable biomass, i.e., the macroinvertebrate biomass in the top 5 cm of sediment excluding invertebrates outside the size range consumed by shorebirds (Lourenço et al., 2017).

Fiddler crab density, sex-ratio, crab/burrow ratio and size class distribution

Burrow counting has been widely used to determine crab density (Altevogt, 1959; Aspey, 1978; Gunther, 1963; Zwarts, 1985; Jordão & Oliveira, 2003), although this method is known to overestimate the number of crabs, from 25% (Macia et al., 2001) up to 46% (Skov et al., 2002), given that one individual can excavate more than one burrow. Recently, in the Bijagós archipelago, Lourenço et al. (2018a) showed that when remotely video recording crab patches, some time after camera set up and associated disturbance, the number of crabs detected in videos rapidly stabilized, suggesting that video recording can be an effective sampling method. Therefore, fiddler crab density was estimated using video cameras in six selected areas, three with low and three with high crab density. In each of these areas, 30 quadrats (70×70 cm) marked with small wooden stakes and a thin wire, were filmed for 4 min each using a Canon PowerShot SX60 HS, with 1980×640 pixel resolution at 25fps. The camera was set on a tripod on the side of the quadrat, and after starting the filming session the observer moved to >50m from the camera until the end of the footage, to avoid any disturbance. Each video was analyzed using the software VLC media player 3.0.6 and as individuals resumed their normal activity, we counted the total number of individuals, the number of burrows and identify the sex of each crab. We also determined the size (carapace width to the nearest mm) of the crabs, using a small ruler previously placed within the quadrat that was used as a reference. We excluded ca.30-60s of the initial and final parts of the film, when the effects of the approaching and departing observer drive away the fiddler crabs into hiding in their burrows. We defined six size classes (see results). Fiddler crabs' biomass was estimated using the regression equations determined by Lourenço et al. (2017). We also determined the crab/burrow ratio.

Sediment sample collection and processing

Sediment sample collection took place in the same areas selected for macroinvertebrate sampling. In total, 30 samples (ca. 40 ml each) of sediment were collected in both low and high crab density areas (15 in each). Samples were air dried after removing all visible particles of detritus. This sediment was then used for determining organic content and fine fraction.

In the laboratory, approximately 5 g of each 40 ml sediment sample was used to determine organic content following the same method described above for determining the biomass of macroinvertebrates. To determine the fine fraction of sediments (i.e. weight of particles < 63 µm/total sample weight) we determined the dry weight of the remaining sediment in each sample. We then hydrated the samples again and used sodium pyrophosphate for six hours to disperse the sediment prior to wet sieving through a 63 µm mesh. Then the dry weight of the material left on the mesh was measured. The weight of the fine fraction was calculated as the difference between the two weights (Quintino et al., 1989).

Shorebird counts

Shorebird density (expressed as number of birds per km²) was calculated from repeated counts during low tide. Sixty-seven plots roughly 250×250m were defined in order to cover a representative part of the Adonga mudflats. The limits of each plot were defined with a set of poles prior to the counts using a GPS (approximate positioning error of ca. 4m). During a single day, five successive counts were performed sequentially on a set of four plots by one observer positioned at the plots' intersection point. This point was reached by boat during ebbing tide, avoiding thus disturbing the birds. Counts were carried out at 1-hour intervals in the period of two hours before and two hours after low tide peak and repeated in each plot two to three times between February and April. In most days, counts involved three observers using zoom-telescopes (20–60×), allowing to singly identify and count each bird within each plot. During the counts we recorded if the birds were feeding or resting in low or high crab density areas, which were easily identified by eye (crabs were only visible by eye in high density areas and strong signs of bioturbation in the top of the sediment were also evident).

Shorebird foraging behavior and diet

Shorebird foraging behavior and diet were studied using video recordings of focal individuals using a Canon PowerShot SX60 HS, with 1980×640 pixel resolution at 25fps. Four species were filmed in areas with low and high crab density: Ringed Plover (*Charadrius hiaticula*), Whimbrel (*Numenius phaeopus*), Grey plover (*Pluvialis squatarola*) and Common redshank (*Tringa totanus*). These were the species more often present in both low and high crab density areas and for which we could achieve a reasonable number of videos. Actively foraging birds were filmed during 2-3 min. If birds stopped feeding or flew away, the video was discarded from further analysis. The videos were analyzed using VLC media player 3.0.6 at low playing speed (down to 1/5 of the original speed). For each focal individual we counted the number of steps, curves (sharp direction changes, > 45°), stops, and feeding attempts (Lourenço et al., 2017). In most videos it was also possible to estimate the success of each foraging attempt by either observing the prey being eaten or by observing swallowing movements. Prey items taken were identified whenever possible and divided in 3 classes: Polychaeta, Bivalvia/Gastropoda and fiddler crabs. Bivalvia and Gastropoda prey were not separated in two classes because it was difficult to distinguish individuals belonging to either of these groups using the videos.

Shorebirds can be divided in visual foragers, i.e. species that use mainly visual cues to search, find and capture prey; tactile foragers, i.e. species that recur mainly to tactile cues using the beak to probe for prey; and mixed foragers that use both visual and tactile cues to find prey (Barbosa & Moreno, 1999; Dias et al., 2009; Lourenço et al., 2017). Furthermore, the shorebird foraging behavior can be divided in sinuous or linear depending on the number of sharp turns performed during the search for prey (Barbosa & Moreno, 1999; Lourenço et al., 2017). Also, shorebirds can be divided depending on the number of stops and steps executed while foraging. Species that mainly search food by scanning the area in front of them and pecking at the substrate surface when they detect a prey are called continuous searchers and species that either probe as they walk or peck at items that they see on the substrate surface are called pause-travel foragers (Barbosa & Moreno, 1999). Taking this into account, the data obtained from videos was used to compare different species in terms of their foraging strategy and diet among the two different crab density classes. For this purpose, we used four behavioral parameters: the number of steps, the ratio of steps.turn⁻¹, the ratio of stops.steps⁻¹ and the rate of feeding attempts.min⁻¹; and five parameters directly related to diet: the ratio of success.attempt⁻¹, the rate of success.min⁻¹, the rate of

Polychaeta consumed.min⁻¹, the rate of Bivalvia/Gastropoda consumed.min⁻¹ and the rate of fiddler crab consumed.min⁻¹.

Data analysis

Bird densities in low and high crab density areas within each 250×250 m plot were calculated by averaging repeated counts within the same day and among all counting days. Only foraging birds were considered for these calculations, birds resting were not included.

All the differences in variables between low and high crab density areas regarding the macroinvertebrate community, fiddler crab populations, sediment samples and shorebird community were tested using a Mann-Whitney U test. This test was selected since our data is non-parametric. For data distributions sufficiently far from normal and for relatively large sample sizes, the Mann-Whitney U test is considerably more efficient than parametric tests like Student's *t*-test.

We used two measurements of diversity, the Shannon Index (H'):

$$\textbf{Equation 1. } H' = \sum_{i=1}^R p_i \ln p_i$$

where p_i is the proportion of individuals belonging to the i^{th} species in the dataset and the exponential Shannon Index ($e^{H'}$):

$$\textbf{Equation 2. } e^{H'} = e^{\sum_{i=1}^R p_i \ln p_i}$$

to determine diversity of both the macroinvertebrate and shorebird communities in areas of low and high crab density. As shown by Jost & González-Oreja (2012), the Shannon Index, although widely used, is not directly compatible with the rules of inference biologists apply to them and conclusions based on them can often be invalid. This may happen because each index calculated for each community has its own units, contrary to species richness, so, technically, comparison across indices should not be possible. In the same study, the authors argue that, nevertheless, the Shannon Index “can be converted to a linear species richness scale by taking their equivalent number of species, the number of equally common, equiprobable species needed to produce a community with the same complexity as that indicated by the original measure. After this conversion, measures can be directly compared with each other. All standard complexity measures of given order q have the same formula when compared:

$$\textbf{Equation 3. } qD = (\sum_{i=1}^R p_i^q)^{1/(1-q)}$$

The most useful diversity measure, and the only one that weighs all species exactly according to their relative contribution to the community, is the limit of this expression as q approaches 1, which equals the exponential of the Shannon index” (Equation 2). Thus, the exponential Shannon Index is more suited to be applied than the “typical” Shannon Index. Nevertheless, we also present the Shannon Index so that our results can, to some degree, be compared with previous works that calculated the “standard” Shannon Index (e.g. Lourenço et al., 2018a).

We also determined the rarefaction curves for the macroinvertebrate communities in low and high crab density areas to allow for an unbiased comparison between the two crab density areas given that, although the number of cores taken in each area was the same, the prevalence of empty cores was different (Hurlbert, 1971). Calculating these curves allowed us to compare the richness of both areas regardless of the sampling effort.

Results

Macroinvertebrate communities in low and high crab density areas

Low crab density areas showed a significantly higher taxonomic richness, Shannon diversity and exponential Shannon when compared with high crab density areas (Table 1). There was a total of 13 species that were only found in low crab density areas and the difference in richness does not depend on the sampling effort (Fig. 2).

Table 1. Mean taxonomic richness and diversity indexes \pm SD calculated per core for the benthic macroinvertebrate community in low (LCD; n=45) and high (HCD; n=45) crab density areas. These variables were compared with Mann-Whitney U tests and we report the significance of the differences (p). Significant differences ($\alpha = 0.05$) are highlighted in bold.

Index	LCD	HCD	p
Taxonomic richness	8.33 (± 2.79)	2.64 (± 1.96)	<0.001
Shannon Diversity	1.74 (± 0.33)	0.77 (± 0.59)	<0.001
Exponential Shannon	6.00 (± 1.97)	2.57 (± 1.68)	<0.001

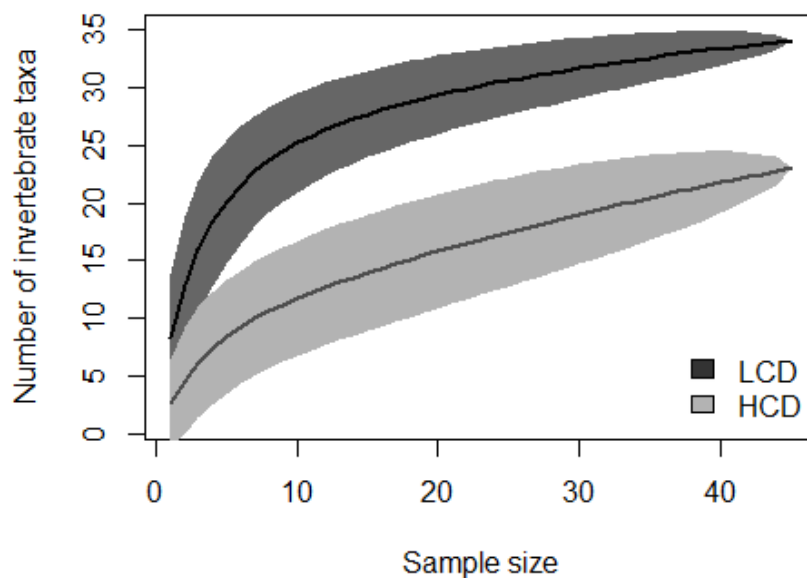


Fig. 2. Invertebrate *taxa* accumulation curves calculated for low (LCD; n=45) and high (HCD; n=45) crab density areas in relation to the number of core samples. The analysis was carried using the lowest possible taxonomic level for each identified *taxon*. The shades around the lines represent the 95% confidence interval.

All classes of invertebrates analyzed were found to have a significantly lower density (Fig.3) as well as lower values of total and harvestable biomass (Fig 4 A and B) in high crab density areas. The most abundant group of macroinvertebrates in low crab density areas were polychaetes, and the most abundant *taxa* were sedentary polychaetes, including Cirratulidae, Capitellidae and Maldanidae. In high crab density areas, polychaetes are also the most abundant macroinvertebrates, although with significantly lower abundances when compared with low crab density areas. The most abundant *taxa*, however, were the bivalves *Pelecycora isocardia* (Dunker, 1845) and *Tagelus adansonii* (Bosc, 1801). Nevertheless, both *taxa* presented a lower density in these areas compared with low crab density areas (Table 2). Moreover, sedentary polychaetes also represented a significant amount of the collected macroinvertebrates in high crab density areas, including Capitellidae, Cirratulidae and Maldanidae individuals, although, again, the density was significantly lower than in low crab density areas. The errant polychaete family Nereidae was also found to be one of the most abundant macroinvertebrates in high crab density areas, with values similar to those from low crab density areas (Table 2). In terms of biomass, the most important macroinvertebrates in low crab density areas were the bivalves *Senilia senilis* (Linnaeus, 1758), *P. isocardia* and *T. adansonii*, the sedentary polychaetes Paraonidae, Capitellidae, Maldanidae and Cirratulidae, the errant polychaetes *Marphysa sanguinea* (Montagu, 1813) and Lumbrineridae and the crustacean *Balsscallichirus balssi* (Monod, 1933). Unsurprisingly, the most important macroinvertebrates in high crab density areas were the fiddler crabs. Moreover, the bivalves *P. isocardia* and *T. adansonii* were also among the main contributors to the macroinvertebrate biomass in these areas although with significantly lower values than in low crab density areas (Table 2). In terms of harvestable biomass the main contributors in low crab density areas were the sedentary polychaetes Capitellidae and Paraonidae, the bivalve *P. isocardia* and the crustacean *B. balssi*. On the other hand, in high crab density areas the most important macroinvertebrates are the fiddler crabs and, to a lesser extent, the bivalve *P. isocardia* (Table 2).

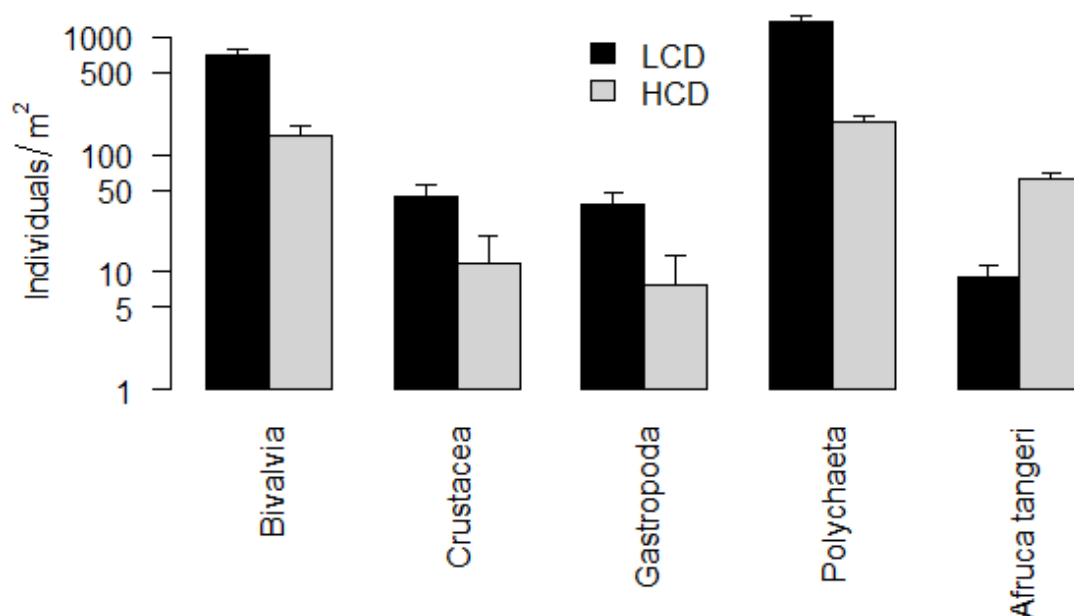


Fig. 3. Mean density \pm SE of the main macroinvertebrate *taxa* sampled in low (LCD) and high crab density areas (HDC). The density estimates of Polychaeta, Bivalvia, Gastropoda and Crustacea (excluding fiddler crabs *A. tangeri*) were calculated from the core sampling (n=90) while the *A. tangeri* density was estimated using video recordings (n=60). Note the logarithmic scale in y-axis.

In terms of abundance, the largest differences among areas were found in the density of sedentary polychaetes Cirratulidae and Maldanidae, the bivalves *Austromacoma nymphaelis* (Lamarck, 1818), *Abra* sp., *S. senilis* and Lucinidae, all of which had lower densities in high crab density areas (Table 2). In terms of total biomass, the major differences were found for the errant polychaetes Glyceridae and Lumbrineridae, for the sedentary polychaetes Capitellidae, Cirratulidae and Paraonidae, for the bivalves *Arcuatula senhousia* (Benson, 1842), *S. senilis* and Lucinidae and for the crustaceans *B. balssi* and *A. tangeri*, all of which presented lower biomass in high crab density areas except for *A. tangeri*. When considering only the harvestable biomass, some *taxa* such as the sedentary polychaete Paraonidae and the bivalve *Abra* sp. considerably lose importance. The largest differences in terms of harvestable biomass were found for the sedentary polychaetes Glyceridae, Capitellidae and Maldanidae, for the bivalves *A. nymphaelis* and Lucinidae and for the crustaceans *B. balssi* and *A. tangeri*. Again, all the above-mentioned *taxa* were found to have a lower biomass in high crab density areas except the fiddler crabs *A. tangeri* themselves.

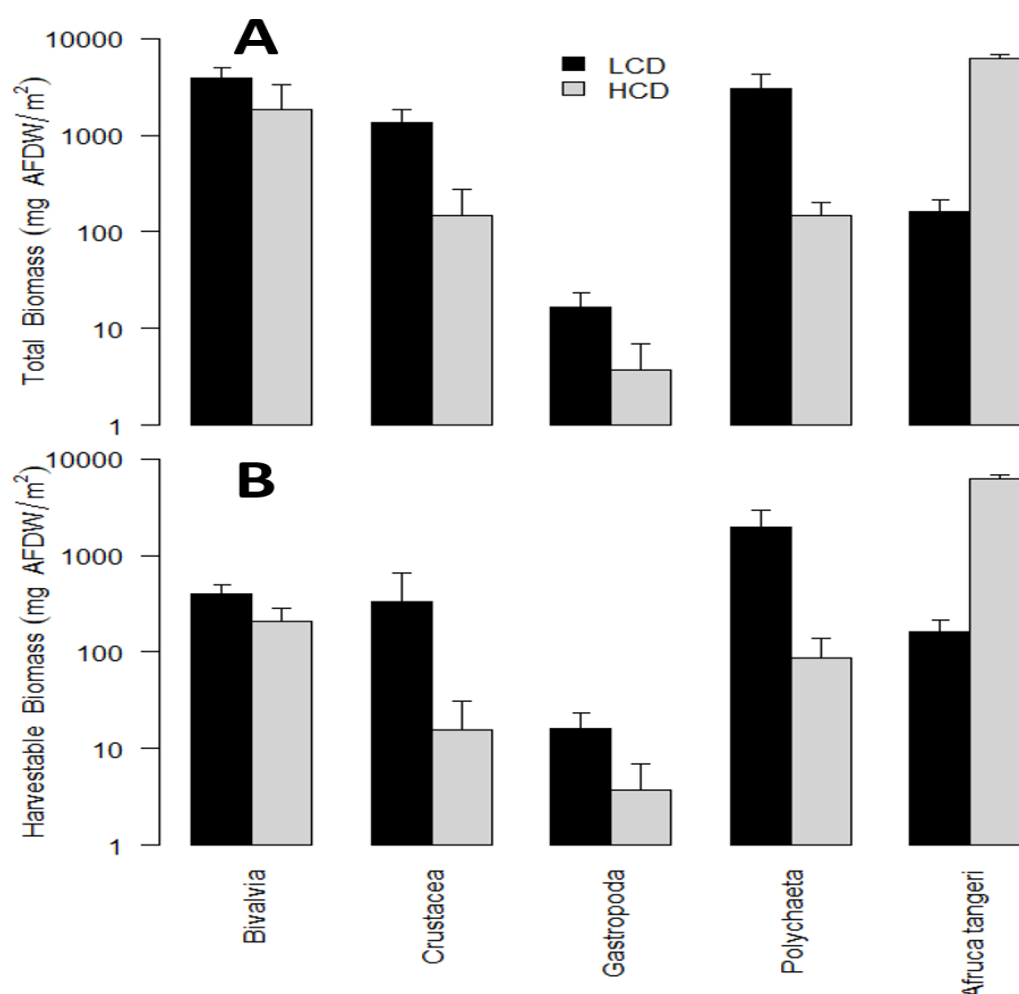


Fig. 4. Mean biomass (measured as mg AFDW/m²) \pm SE of the main macroinvertebrate *taxa* sampled in both low (LCD) and high (HCD) crab density areas. The biomass estimates of Polychaeta, Bivalvia, Gastropoda and Crustacea (excluding *A. tangeri*) were calculated from the core sampling (n=90) while the *A. tangeri* biomass was estimated using the video recordings (n=60) and regression equations calculated in Lourenço et al. (2017). A – Total biomass estimates using all samples collected up to a depth of 20 cm. B – Estimates of harvestable biomass for shorebirds using samples collected only in the top 5 cm of sediment excluding invertebrates outside the size range consumed by shorebirds (based in Lourenço et al. 2017). Note the logarithmic scale in y-axis.

Table 2. Mean density (individuals/m²), total biomass (mg AFDW/m²) and harvestable biomass (mg AFDW/m²) in the top 5 cm of sediment; only invertebrates in the size range consumed by shorebirds) \pm SE of all macroinvertebrate *taxa* estimated for low (LCD) and high (HCD) crab density areas. Estimates calculated from the core sampling (n=90), except for *A. tangeri*. *Afruca tangeri* density estimated using the video recordings (n=60). These variables were compared with Man-Whitney U tests and we report the significance of the differences (*p*). Significant differences ($\alpha = 0.05$) are highlighted in bold.

Taxa	Density			Total biomass			Harvestable biomass		
	LCD	HCD	<i>p</i>	LCD	HCD	<i>p</i>	LCD	HCD	<i>p</i>
Polychaeta (total)	1324.33 (± 193.16)	188.63 (± 23.78)	<0.001	3090.38 (± 1252.28)	147.58 (± 55.21)	<0.001	1952.47 (± 1042.95)	88.07 (± 52.39)	<0.001
Errantia (total)	222.03 (± 25.69)	64.84 (± 12.05)	<0.001	1116.67 (± 329.86)	73.11 (± 52.65)	<0.001	216.20 (± 71.68)	72.64 (± 52.66)	<0.001
Eunicidae	17.68 (± 3.69)	3.93 (± 1.82)	<0.001	245.29 (± 106.15)	18.42 (± 17.51)	<0.001	30.64 (± 23.63)	18.42 (± 17.51)	0.050
<i>Eunice</i> sp.	7.86 (± 3.79)	0	0.043	2.87 (± 1.77)	0	0.082	2.87 (± 1.77)	0	0.082
<i>Marphysa sanguinea</i>	19.65 (± 6.21)	1.96 (± 1.96)	0.008	709.67 (± 309.03)	52.52 (± 52.52)	0.007	82.64 (± 70.65)	52.52 (± 52.52)	0.179
Glyceridae	37.33 (± 9.93)	1.96 (± 1.96)	<0.001	65.33 (± 18.01)	0.39 (± 0.39)	<0.001	51.59 (± 14.51)	0.39 (± 0.39)	<0.001
Lumbrineridae	33.40 (± 7.59)	1.96 (± 1.96)	<0.001	245.59 (± 69.51)	7.43 (± 7.43)	<0.001	51.75 (± 21.43)	7.43 (± 7.43)	0.026
Nephtyidae	35.37 (± 9.89)	11.79 (± 4.53)	0.083	50.66 (± 32.62)	1.49 (± 1.08)	0.061	6.90 (± 2.88)	1.49 (± 1.08)	0.291
Nereidae	41.26 (± 12.12)	33.40 (± 8.56)	0.956	10.49 (± 3.76)	7.74 (± 3.01)	1	10.08 (± 3.76)	7.27 (± 2.99)	1
Onuphidae	1.96 (± 1.96)	0	0.328	1.74 (± 1.74)	0	0.328	1.74 (± 1.74)	0	0.328
Syllidae	19.65 (± 5.54)	3.93 (± 2.75)	0.014	6.98 (± 2.49)	0.79 (± 0.57)	0.013	2.20 (± 1.08)	0.79 (± 0.57)	0.251
Sedentaria (total)	1051.21 (± 171.98)	119.86 (± 20.49)	<0.001	1943.59 (± 1028.61)	71.21 (± 21.35)	<0.001	1717.89 (± 1033.52)	14.54 (± 3.86)	<0.001
Capitellidae	113.96 (± 19.79)	51.09 (± 13.33)	0.003	781.18 (± 710.49)	37.12 (± 18.06)	<0.001	759.50 (± 710.97)	7.49 (± 2.61)	0.017
Cirratulidae	538.38 (± 158.34)	33.40 (± 9.44)	<0.001	131.67 (± 37.37)	4.59 (± 1.66)	<0.001	83.61 (± 30.69)	2.95 (± 1.13)	<0.001
Maldanidae	345.82 (± 42.14)	31.44 (± 9.39)	<0.001	209.79 (± 33.57)	24.23 (± 12.23)	<0.001	91.74 (± 22.15)	4.11 (± 2.22)	<0.001
Orbiniidae	25.54 (± 7.76)	0	<0.001	21.29 (± 10.05)	0	<0.001	9.65 (± 5.60)	0	0.006
Paraonidae	51.09 (± 13.62)	3.93 (± 3.93)	<0.001	819.41 (± 770.82)	5.27 (± 5.27)	<0.001	781.49 (± 771.50)	0	0.002
Terebellidae	1.96 (± 1.96)	0	0.328	1.55 (± 1.55)	0	0.328	1.55 (± 1.55)	0	0.328

Table 2 continued.

Taxa	Density			Total biomass			Harvestable biomass		
	LCD	HCD	<i>p</i>	LCD	HCD	<i>p</i>	LCD	HCD	<i>p</i>
Polychaeta (cont.)									
Polychaeta incertae sedis (total)	7.85 (±3.79)	1.96 (±1.96)	0.173	4.95 (±3.52)	0.88 (±0.88)	0.179	4.85 (±3.52)	0.88 (±0.88)	0.320
Magelonidae	7.85 (±3.79)	1.96 (±1.96)	0.173	4.95 (±3.52)	0.88 (±0.88)	0.179	4.85 (±3.52)	0.88 (±0.88)	0.320
Polychaeta indet.	17.68 (±15.79)	0	0.1596	3.87 (±3.06)	0	0.159	3.87 (±3.06)	0	0.159
Bivalvia (total)	711.9 (±82.69)	145.40 (±31.31)	<0.001	3932.64 (±1087.37)	1837.81 (±1474.81)	<0.001	405.91 (±95.04)	205.66 (±81.19)	<0.001
<i>Abra</i> sp.	23.57 (±10.29)	1.96 (±1.96)	0.048	85.63 (±39.65)	30.91 (±30.91)	0.058	39.83 (±17.01)	0	0.012
<i>Arcuatula senhousia</i>	21.61 (±6.97)	3.93 (±3.93)	0.009	9.23 (±3.70)	0.33 (±0.33)	0.007	6.41 (±2.75)	0.33 (±0.33)	0.025
<i>Austromacoma nympha</i>	25.54 (±7.76)	1.96 (±1.96)	0.004	28.49 (±9.84)	1.18 (±1.18)	0.003	21.76 (±7.99)	1.18 (±1.18)	0.013
<i>Loripes</i> sp.	1.96 (±1.96)	0	0.328	52.62 (±52.62)	0	0.328	0	0	-
<i>Pelecypoda isocardia</i>	408.69 (±57.13)	78.59 (±20.88)	<0.001	376.12 (±100.49)	208.63 (±86.96)	<0.001	261.74 (±80.56)	179.22 (±79.44)	0.002
<i>Senilia senilis</i>	39.29 (±8.22)	1.96 (±1.96)	<0.001	3113.8 (±1093.62)	79.56 (±79.56)	<0.001	9.09 (±3.38)	0	0.006
<i>Striarca lactea</i>	11.78 (±7.22)	0	0.082	15.72 (±10.99)	0	0.082	0.02 (±0.02)	0	0.328
<i>Tagelus adansonii</i>	72.70 (±20.32)	47.16 (±11.79)	0.813	156.15 (±96.93)	1515.06 (±1473.39)	0.901	9.61 (±6.77)	23.07 (±9.24)	0.717
Lucinidae indet.	106.10 (±16.29)	9.82 (±4.19)	<0.001	94.86 (±41.92)	2.14 (±1.29)	<0.001	47.45 (±14.17)	1.87 (±1.28)	<0.001
Gastropoda (total)	37.33 (±10.32)	7.86 (±6.17)	0.002	16.44 (±7.09)	3.67 (±3.35)	0.001	16.11 (±7.10)	3.67 (±3.35)	0.002
<i>Bulla</i> sp.	23.58 (±9.49)	7.86 (±6.17)	0.049	13.66 (±7.04)	3.67 (±3.35)	0.047	13.66 (±7.04)	3.67 (±3.35)	0.047
<i>Retusa</i> sp.	3.93 (±2.75)	0	0.159	0.67 (±0.47)	0	0.159	0.67 (±0.47)	0	0.159
<i>Turbonilla</i> sp.	1.96 (±1.96)	0	0.328	0.33 (±0.33)	0	0.328	0.33 (±0.33)	0	0.328
<i>Rissoidea</i> indet.	3.93 (±2.75)	0	0.159	1.18 (±0.90)	0	0.159	0.84 (±0.84)	0	0.328

Table 2 continued.

Taxa	Density			Total biomass			Harvestable biomass		
	LCD	HCD	<i>p</i>	LCD	HCD	<i>p</i>	LCD	HCD	<i>p</i>
Gastropoda (cont.)									
<i>Rissoela</i> sp.	1.96 (±1.96)	0	0.328	0.59 (±0.59)	0	0.328	0.59 (±0.59)	0	0.328
Gastropoda indet.	1.96 (±1.96)	0	0.328	0.02 (±0.02)	0	0.328	0.02 (±0.02)	0	0.328
Crustacea (total except <i>A. tangeri</i>)	43.23 (±11.46)	11.79 (±8.71)	0.008	1374.15 (±476.21)	149.06 (±126.87)	0.001	333.54 (±317.49)	15.44 (±15.20)	0.396
<i>Balsscallichirus balssi</i>	35.37 (±8.62)	7.86 (±5.49)	0.002	1346.07 (±472.43)	32.87 (±25.33)	<0.001	333.54 (±317.49)	9.22 (±8.98)	0.386
<i>Pachygrapsus gracilis</i>	0	1.96 (±3.93)	0.328	0	116.16 (±116.16)	0.328	0	6.23 (±6.23)	0.328
Alpheidae	7.85 (±3.79)	0	0.043	28.08 (±17.77)	0	0.043	0	0	-
<i>Afruca tangeri</i>	9.12 (±2.04)	62.44 (±6.31)	<0.001	161.41 (±53.99)	6311.97 (±490.37)	<0.001	161.41 (±53.99)	6311.97 (±490.37)	<0.001

Fiddler crab sex-ratio, crab/burrow ratio and size-class distribution

We determined the sex and measured a total of 1044 crabs. The size class distribution differed between areas with low and high crab densities. In high crab density areas we found individuals belonging to all six size-classes and small individuals (<0.5 cm) comprised less than 20% of the sampled population. Conversely, in low crab density areas we only registered crabs belonging to the four smallest classes (Fig. 5), with crabs measuring <0.5 cm comprising almost 50% of all individuals measured. In both areas, the two smallest classes were more prevalent with the 0.5-1 cm class dominating in the high crab density areas and the 0-0.5 cm class dominating in the low crab density areas.

The sex-ratio was found to be female biased in high crab density areas and male biased in low crab density areas (Table 3) although there were no significant differences among areas. There was a high proportion of crabs, about one third (357 individuals), whose sex could not be determined due to their small size. No significant differences in size were found between sexes (Mann-Whitney Test, $W = 57792$, $p = 0.681$; Fig. 6).

The crab/burrow ratio could only be determined for high crab density areas since in low crab density areas there was a high density of holes of unknown origin (either from crabs or other organisms, such as polychaetes and bivalves). Crab/burrow ratio was estimated to be 0.28 (±0.12 SD, $n=29$ videos).

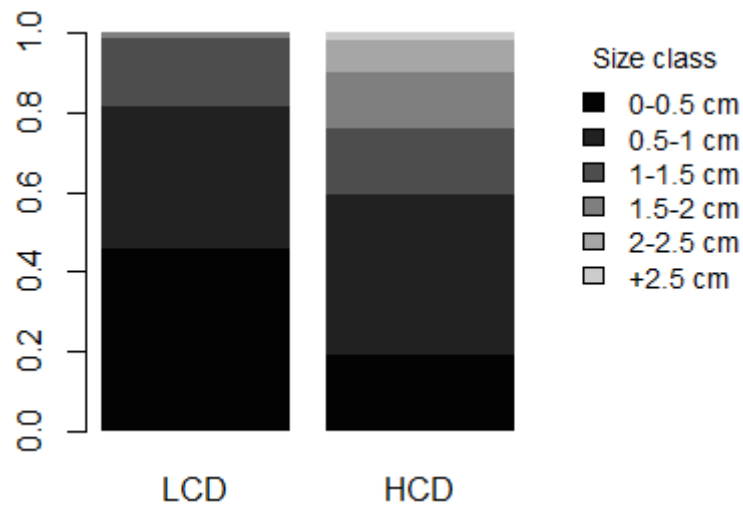


Fig. 5. Size class proportion of fiddler crab *Afruca tangeri* populations in low (LCD) and high crab density (HCD) areas (n=1044 individuals).

Table 3. Sex-ratio of fiddler crab *Afruca tangeri* populations in low (LCD) and high crab density (HCD) areas. Only individuals with a carapace width >1 cm were included in the analysis, in order to exclude all crabs that could not be sexed. The p was calculated using a Chi-Squared Test (χ^2 -squared = 2, df = 1).

Area	Sex-ratio	p
HCD (n=376)	1 F : 0.88 M	0.214
LCD (n=23)	1 F : 1.81 M	

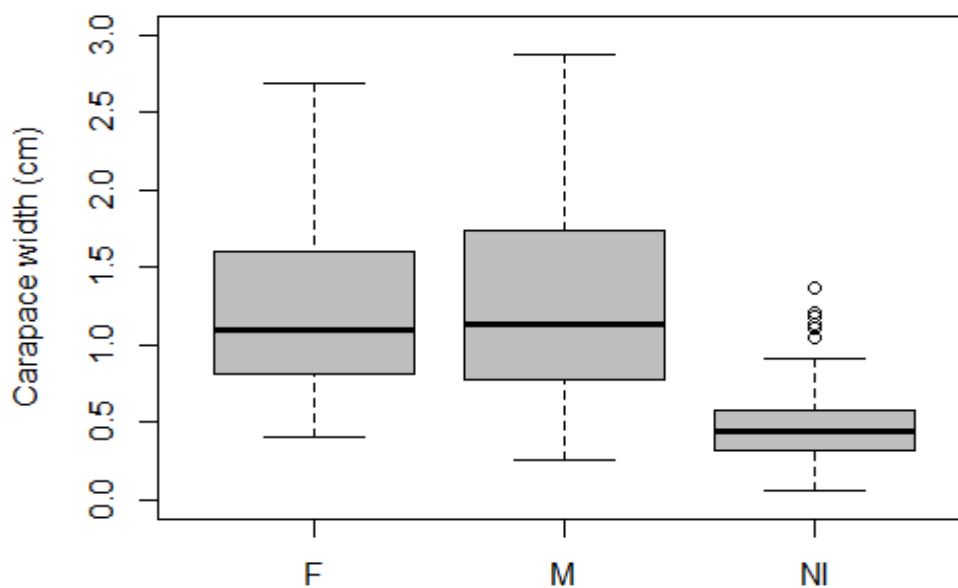


Fig. 6. Carapace width of female (F, n=360), male (M, n=327) and unknown sex (NI, n=357) fiddler crabs *Afruca tangeri*.

Sediment characteristics

Organic matter content and fine fraction of the sediment were significantly higher in high crab density areas. These two characteristics were also found to have a strong positive correlation (Pearson Correlation = 0.856, $p < 0.001$) (Table 4).

Table 4. Mean \pm SD organic matter content (% AFDW) and fine fraction of the sediment samples collected in low (LCD) and high crab density (HCD) areas. These variables were compared with Mann-Whitney U tests and we report the significance of the differences (p). Significant differences ($\alpha = 0.05$) are highlighted in bold.

Variable	LCD (n=15)	HCD (n=15)	p
AFDW (%)	2.78 (± 2.01)	5.98 (± 2.66)	<0.001
Fine fraction (%)	17.95 (± 12.44)	32.65 (± 12.18)	0.003

Shorebird communities in low and high crab density areas

The shorebird community of low crab density areas showed a higher taxonomic richness, Shannon diversity and exponential Shannon when compared with high crab density areas (Table 5). The 18 most common shorebird species counted are illustrated in Fig. 7.

Table 5. Mean richness and diversity indexes \pm SD calculated for the shorebird community in low (LCD) and high (HCD) crab density areas using the plot counts (n=67). These variables were compared with Mann-Whitney U tests and we report the significance of the differences (p). Significant differences ($\alpha = 0.05$) are highlighted in bold.

Index	LCD	HCD	p
Species richness	12.06 (± 3.87)	10.65 (± 3.31)	0.013
Shannon Diversity	1.72 (± 0.44)	1.57 (± 0.45)	0.045
Exponential Shannon	5.99 (± 1.94)	5.24 (± 1.87)	0.045

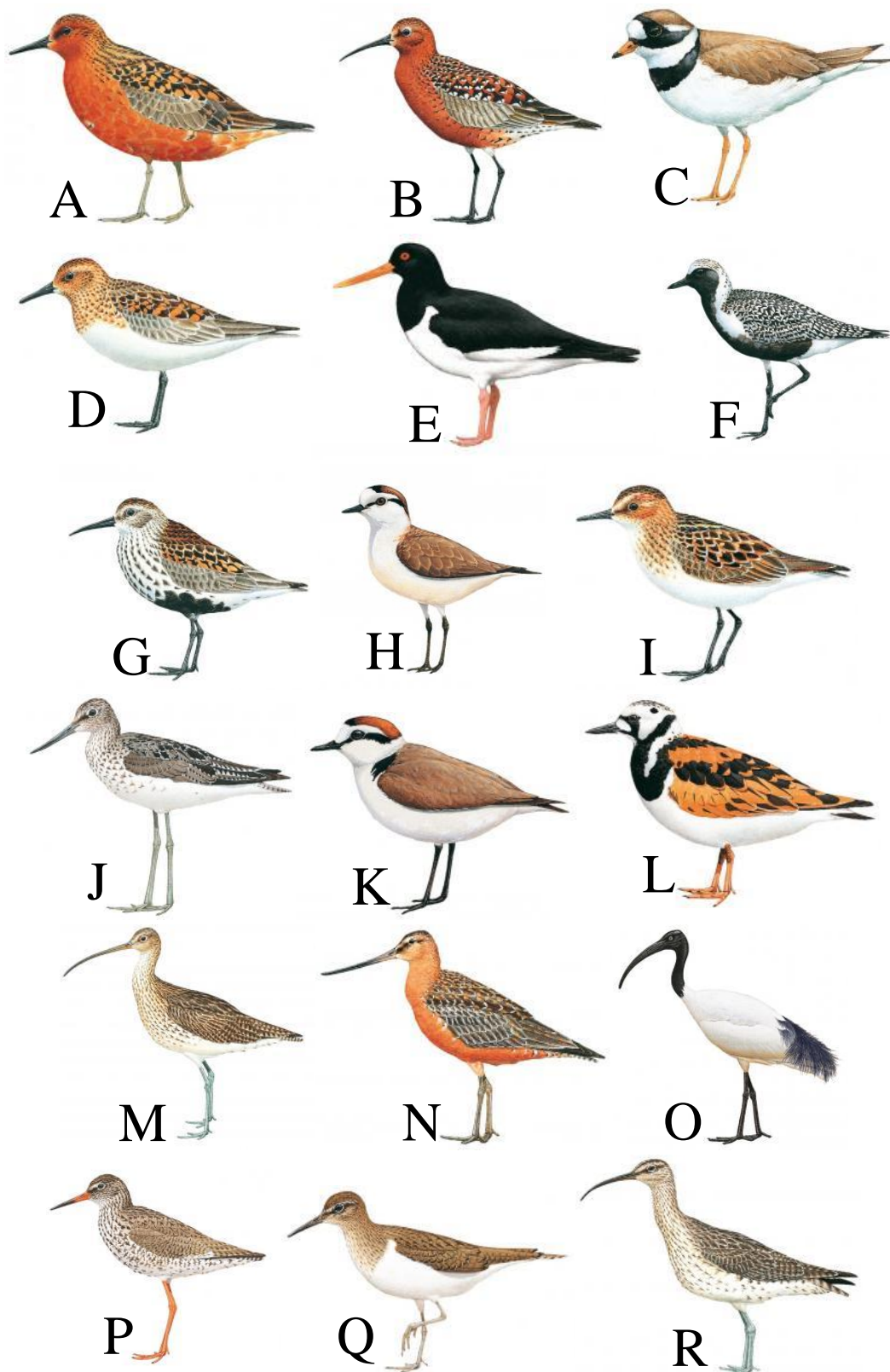


Fig. 7. Illustrations of the 18 most common shorebird species counted. All the illustrations and their rights are owned by ©2019 HBW Alive: Handbook of the Birds of the World Alive (www.hbw.com). Bird images are NOT to scale. A – Red knot; B – Curlew sandpiper; C – Ringed plover; D – Sanderling; E – Eurasian Oystercatcher; F – Grey plover; G – Dunlin; H – White-fronted plover; I – Little stint; J – Common greenshank; K – Kentish plover; L – Ruddy turnstone; M – Eurasian curlew; N – Bar-tailed godwit; O – Sacred ibis; P – Common redshank; Q – Common sandpiper; R – Whimbrel.

Twelve out of the 18 most common shorebird species studied showed significant differences in terms of density among the two different crab density areas (Fig. 8, Table 6). Among this, seven species showed higher densities in low crab density areas (Sanderling *Calidris alba*, Dunlin *Calidris alpina*, Red knot *Calidris canutus*, Curlew sandpiper *Calidris ferruginea*, Little stint *Calidris minuta*, Kentish plover *Charadrius alexandrinus* and Ringed plover *Charadrius hiaticula*), while five species showed the opposite pattern (Common sandpiper *Actitis hypoleucos*, Eurasian curlew *Numenius arquata*, Whimbrel *Numenius phaeopus*, Sacred ibis *Threskiornis aethiopicus* and Common redshank *Tringa totanus*). For the remaining six species (Ruddy turnstone *Arenaria interpres*, White-fronted plover *Charadrius marginatus*, Eurasian oystercatcher *Haematopus ostralegus*, Bar-tailed godwit *Limosa lapponica*, Grey plover *Pluvialis squatarola* and Common greenshank *Tringa nebularia*) no significant differences were evident. The largest differences (more than tenfold) were found for Common sandpiper, Red knot and Ringed plover.

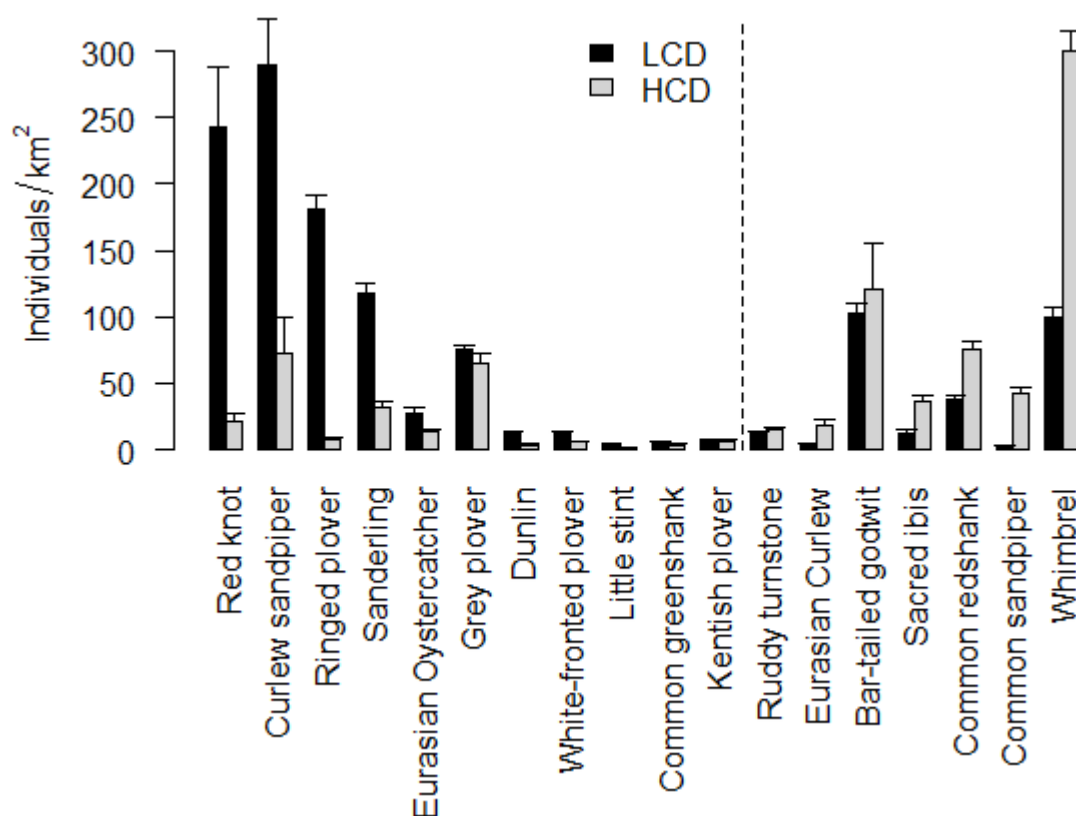


Fig. 8. Mean densities (individuals/km²) \pm SE of the most frequent shorebird species recorded in low (LCD) and high (HCD) crab density areas. The vertical line separates species that have higher densities in low crab density areas from species with higher densities in high crab density areas.

Table 6. Mean densities (individuals/km²) \pm SE of the most frequent shorebird species recorded in the low (LCD) and high (HCD) crab density areas. Densities between areas were compared with Mann-Whitney U tests and we report the significance of the differences (*p*). Significant differences ($\alpha = 0.05$) are highlighted in bold.

Species	Density (inds/km ²)		
	LCD	HCD	<i>p</i>
Red knot <i>Calidris canutus</i>	242.38 (± 46.15)	21.75 (± 5.28)	<0.001
Curlew sandpiper <i>Calidris ferruginea</i>	289.37 (± 35.09)	73.17 (± 26.19)	<0.001
Ringed plover <i>Charadrius hiaticula</i>	181.22 (± 10.81)	7.63 (± 1.18)	<0.001
Sanderling <i>Calidris alba</i>	118.27 (± 7.27)	32.08 (± 4.17)	<0.001
Eurasian oystercatcher <i>Haematopus ostralegus</i>	27.99 (± 3.87)	13.70 (± 2.09)	0.202
Grey plover <i>Pluvialis squatarola</i>	74.87 (± 4.19)	65.43 (± 7.58)	0.091
Dunlin <i>Calidris alpina</i>	11.92 (± 1.96)	3.30 (± 1.26)	<0.001
White-fronted plover <i>Charadrius marginatus</i>	12.36 (± 1.14)	5.97 (± 0.87)	0.085
Little stint <i>Calidris minuta</i>	4.38 (± 0.73)	0.86 (± 0.46)	<0.001
Common greenshank <i>Tringa nebularia</i>	4.96 (± 0.58)	3.57 (± 0.91)	0.076
Kentish plover <i>Charadrius alexandrinus</i>	6.77 (± 0.75)	5.51 (± 1.45)	0.021
Ruddy turnstone <i>Arenaria interpres</i>	12.61 (± 1.45)	15.28 (± 2.00)	0.878
Eurasian curlew <i>Numenius arquata</i>	4.37 (± 0.53)	18.98 (± 4.02)	0.025

Table 6 continued.

Species	Density (inds/km ²)		
	LCD	HCD	<i>p</i>
Bar-tailed godwit <i>Limosa lapponica</i>	102.32 (±7.69)	121.43 (±34.14)	0.539
Sacred ibis <i>Threskiornis aethiopicus</i>	12.77 (±2.19)	36.17 (±4.46)	0.001
Common redshank <i>Tringa totanus</i>	37.88 (±2.82)	75.02 (±7.06)	0.015
Common sandpiper <i>Actitis hypoleucos</i>	3.20 (±0.51)	42.54 (±4.89)	<0.001
Whimbrel <i>Numenius phaeopus</i>	99.68 (±6.97)	300.07 (±14.59)	<0.001

Shorebird foraging behavior and diet

We filmed a total of 139 focal foraging birds corresponding to ca. 7 h of film. The major difference found on the foraging behavior of the four species studied between low and high crab density areas was the pecking rate, which was significantly higher in areas with low crab density (for all species except Grey plover; Tables 7 and 8). The Ringed plover showed a higher success per peck in high crab density areas, while the Whimbrel showed a higher stops.steps⁻¹ rate in these areas. The Common redshank took more steps per minute and had a less sinuous search behavior (less curves.steps⁻¹) in high crab density areas while no significant differences were found in the foraging behavior of the Grey plover (Tables 7 and 8).

In terms of diet, few differences were found among areas with different crab densities (Tables 7 and 8 / Fig. 9). The Whimbrel fed more frequently on Bivalvia/Gastropoda in low crab density areas while in high crab density areas *A. tangeri* is the main prey item taken. The Grey plover consumed more fiddler crabs in high crab density areas as well as more Bivalvia/Gastropoda prey. The Common redshank and Ringed plover did not show significant differences in terms of diet composition between low and high crab density areas.

Table 7. Behavioral parameters (means \pm SD, samples sizes in parenthesis) of foraging shorebirds (Ringed plover and Whimbrel) video-recorded in areas with low (LCD) and high (HCD) crab densities. Parameters were compared with Mann-Whitney U tests and we report the significance of the differences (p). Significant differences ($\alpha = 0.05$) are highlighted in bold.

Variables	Ringed plover			Whimbrel		
	LCD (n=18)	HCD (n=18)	p	LCD (n=23)	HCD (n=23)	p
Steps.min ⁻¹	128.38 (± 29.60)	119.68 (± 29.60)	0.170	98.42 (± 39.74)	89.09 (± 42.86)	0.617
Curves.steps ⁻¹	0.09 (± 0.03)	0.08 (± 0.03)	0.389	0.05 (± 0.03)	0.04 (± 0.04)	0.130
Stops.steps ⁻¹	0.18 (± 0.06)	0.16 (± 0.09)	0.097	0.005 (± 0.008)	0.01 (± 0.03)	0.016
Pecking.min ⁻¹	21.19 (± 7.15)	13.47 (± 8.45)	0.003	6.56 (± 4.28)	2.53 (± 3.48)	<0.001
Success.peck ⁻¹	0.09 (± 0.09)	0.15 (± 0.09)	0.048	0.14 (± 0.18)	0.23 (± 0.26)	0.395
Success.min ⁻¹	1.68 (± 1.41)	1.53 (± 0.90)	0.764	0.98 (± 1.39)	0.65 (± 1.10)	0.647
Fiddler crabs.min ⁻¹	0.02 (± 0.08)	0.09 (± 0.19)	0.163	0.32 (± 0.58)	0.42 (± 0.42)	0.139
Polychaeta.min ⁻¹	0.89 (± 1.20)	0.86 (± 1.01)	0.748	0.01 (± 0.07)	0	0.339
Bivalvia/Gastropoda.min ⁻¹	0.27 (± 0.34)	0.20 (± 0.22)	0.757	0.56 (± 0.93)	0.22 (± 1.04)	0.004

Table 8. Dietary parameters (means \pm SD, samples sizes in parenthesis) of foraging shorebirds (Grey plover and Common redshank) video-recorded in areas with low (LCD) and high (HCD) crab densities. Parameters were compared with Mann-Whitney U tests and we report the significance of the differences (p). Significant differences ($\alpha = 0.05$) are highlighted in bold.

Variables	Grey plover			Common redshank		
	LCD (n=16)	HCD (n=16)	p	LCD (n=10)	HCD (n=15)	p
Steps.min ⁻¹	77.90 (± 39.98)	87.58 (± 44.38)	0.270	132.18 (± 29.76)	186.09 (± 77.65)	0.041
Curves.steps ⁻¹	0.07 (± 0.03)	0.06 (± 0.03)	0.274	0.09 (± 0.03)	0.07 (± 0.07)	0.037
Stops.steps ⁻¹	0.12 (± 0.04)	0.13 (± 0.08)	0.867	0 (± 0.001)	0 (± 0.001)	0.552

Table 8 continued.

Variables	Grey plover			Common redshank		
	LCD (n=16)	HCD (n=16)	<i>p</i>	LCD (n=10)	HCD (n=15)	<i>p</i>
Pecking.min ⁻¹	6.67 (±6.11)	6.46 (±5.59)	0.926	34.27 (±12.86)	11.32 (±7.87)	<0.001
Success.peck ⁻¹	0.25 (±0.22)	0.18 (±0.26)	0.172	0.08 (±0.12)	0.11 (±0.13)	0.486
Success.min ⁻¹	1.22 (±1.79)	0.88 (±1.61)	0.149	1.64 (±1.49)	1.07 (±1.18)	0.398
Fiddler crabs.min ⁻¹	0	0.23 (±0.39)	0.009	0.05 (±0.17)	0.07 (±0.19)	0.844
Polychaeta.min ⁻¹	0.12 (±0.19)	0.04 (±0.17)	0.108	0	0.13 (±0.39)	0.263
Bivalvia/Gastropoda.min ⁻¹	0.20 (±0.19)	0.23 (±0.83)	0.029	0.07 (±0.14)	0.02 (±0.09)	0.404

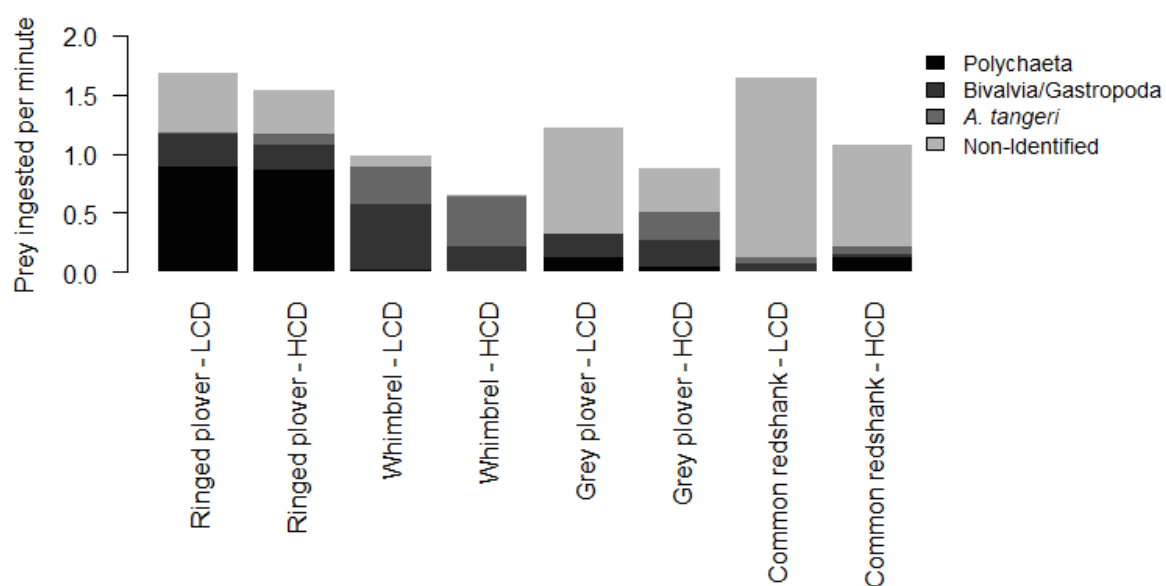


Fig. 9. Prey ingested per minute and proportion of prey group ingested in low (LCD) and high (HCD) crab density areas.

Discussion

Differences in macroinvertebrate communities between low and high crab density areas

The results suggest that fiddler crabs have a strong effect on the structure (composition and abundance) of the remaining macroinvertebrate community. The richness and diversity of the benthic macroinvertebrate community are much lower in high crab density areas. Moreover, there were 13 species that were never sampled in high crab density areas. Additionally, almost all invertebrate *taxa* studied showed drastically lower density and biomass in high crab density areas. Many species were two to six times less abundant in high crab density areas. Even the most abundant species in areas with high crab density showed lower abundances compared to low crab density areas.

Similar impacts have been recorded for meiofaunal organisms and may result either from direct effects, such as predation, or indirect effects, such as disturbance or competition for food (Hoffman et al, 1984; Reinsel, 2004; Weis and Weis, 2004). In this case, predation is the less likely hypothesis since fiddler crabs feed mainly on vegetable detritus, microalgae, nematodes and bacteria (Emmerson & McGwynne, 1992; Lee, 1997; Kristensen & Alongi, 2006; Kristensen, 2008). Since fiddler crabs share the same preferred food source with many species of the remaining macroinvertebrate community, competition is a likely mechanism reducing the diversity and density of the macroinvertebrate community in high crab density areas (Kruitwagen et al., 2010).

The disturbance effect caused by the burrowing activity of fiddler crabs can also have deep impacts in the macrobenthos due to changes in sediment topography and biogeochemistry (Mouton & Felder, 1996; Botto & Iribarne, 2000; Kristensen, 2008). The physical stability of other macroinvertebrate burrows can be compromised as crabs may dig their complex burrow network down to 40 cm, making the presence of other macroinvertebrates more difficult in these areas (Koretsky et al., 2002; Lim, 2006). This is the case for errant polychaetes, for instance, which rely on migrations through the sediment to search for food (Tamaki, 1985). Bioturbation performed by the fiddler crabs can offer a physical challenge for movement representing thus an important disturbance factor leading to a lower abundance of these organisms. Previous studies have also shown that bioturbation may lead to a reduction on the survival rate of mobile benthos, such as errant polychaetes (Wilson, 1981; Jensen, 1985; Levinton, 1985; Tamaki, 1988), and sessile benthos, such as sedentary polychaetes and bivalves (Stevens, 1928; Dorsey & Synnot, 1980; Posey, 1986), by reducing their refuge areas and ultimately excluding them. Bioturbation promoted by fiddler crabs may also be the factor leading to the lower densities of gastropods and crustaceans in high crab density areas, as crab activity may decrease the survivability of gastropods (Pillay et al., 2007) and inhibit the burrowing behavior of other crustaceans (Banner & Banner, 1966; Abele & Felgenhauer, 1982; Tamaki, 1988).

Bioturbation also causes significant changes to the sediment characteristics. The increment in the area of exposed sediment to the air and water facilitates the erodibility of the particles, leading to an increase in the fine fraction (Botto & Iribarne, 2000). Also, there may be an increase in the organic matter content, since the crabs force the ascension of deep organic matter to the surface, which promotes the growth and activity of bacteria, further increasing the organic matter content (Katz, 1980; Montague, 1980a,b; Bertness, 1985; Gutiérrez et al., 2006; Kristensen, 2008). Our results showed that both organic matter content and fine fraction of the sediment are significantly higher in high crab density areas, which strongly agrees with the previous findings. Nevertheless, the increase in organic matter can also be strictly related with the increase in the fine fraction. The decrease in the sediment particle size alone may be creating conditions for the increase in organic matter content (Evans et al., 1990). It is difficult to determine the main reason behind the increase in organic matter as either the bioturbation performed

by the fiddler crabs or the increase in the fine fraction can be the direct cause. For years now, macroinvertebrate communities' distribution has been known to be greatly influenced by sediment characteristics (Pearson & Rosenberg, 1978; Beukema, 1988; Raffaelli & Hawkins, 1996; Ysebaert & Herman, 2002). Rodrigues et al. (2006) has shown that sampling sites characterized either by high fine contents or high organic matter content present in general lower macroinvertebrate species richness and abundance, although the sediment descriptors alone do not explain the general pattern of distribution and other factors, such as the biogenic fraction, are likely involved. Specially, the increase in organic matter may prevent the macroinvertebrate community from achieving their potential maximum richness, diversity and density (Bolam et al., 2004). Moreover, meio- and macrofauna often respond similarly when affected by disturbance and organic matter enrichment caused for example by the fiddler crabs' bioturbation. When the levels of disturbance and organic matter are low, the maximum diversity is observed but increasingly higher levels of both variables tend to lead to a decrease in meio- and macrofaunal diversity (Austen & Widdicombe, 2006). Since high density of fiddler crab populations significantly increases the organic matter content and the disturbance, as expected, the remaining macroinvertebrate community presents lower richness, diversity, density and biomass.

The preferences regarding sediment fine fraction for each *taxa* can also be affecting the results. Most polychaetes and bivalves prefer a fine fraction and organic content of sediment similar to what we found in low crab density areas. Preferences for polychaetes include a fine fraction of 20% for Capitellidae and Orbiniidae (Anderson, 2008), and a fine fraction of 18% and organic matter content of 2% for Paraonidae and Cirratulidae (Martins et al., 2013). For bivalves some optimal values assessed in previous studies for these characteristics include a fine fraction around 20% for *S. senilis* (Honkoop et al., 2008), 10-26% for Tellinidae and 7-15% for Veneridae (the family of *Pelecypora isocardia*) (Anderson, 2008).

The invasive species *A. senhousia* had been previously recorded for the mudflats of the Bijagós archipelago (Lourenço et al., 2018b). This species is an opportunistic suspension feeder with high reproductive capacity and fast growth rate, capable of achieving high population densities and forming large mats (Crooks 1996; Mistri et al., 2004; Hayward et al., 2008) but it appears to have a low density in the Adonga mudflats for now. The density and biomass of this invasive species are especially low in high crab density areas where the disturbance driven by fiddler crabs may be delaying the expansion of *A. senhousia*. Still, the presence of this invasive species was recorded in 20.0% (n=45) of all cores collected in areas with low crab density in this region of the Orango National Park.

Although many differences have been found in the benthic macroinvertebrate communities inhabiting low and high crab density areas, for 17 *taxa* we found no significant differences. Most of these *taxa* were relatively rare and thus results are less conclusive. An increase in sampling effort would be needed to properly sample these invertebrates. Still, for some of the relatively abundant *taxa*, the impacts of fiddler crabs seem to be negligible. This is the case for Nereidae and Nephtyidae polychaetes which are very versatile organisms and have been shown to have a wide range of sediment type preference ranging from low to high fine particle content depending on the species (Kristensen, 1998; Meißner et al., 2008). Also, some bivalve genera have a wide variety of preferences regarding sediment type like *Abra* (Alexander et al., 1993; Thiébaud et al., 1997) and *Tagellus* (Holland & Dean, 1977) and thus, sediment variables are a poor indicator of the spatial structure of both *taxa*.

Some of our results may also be influenced by factors not analyzed in this study. Many variables either biotic, such as salinity and currents (e.g. van der Meer, 1991; Ysebaert et al., 2002; Compton et al., 2013), or biotic such as interaction with other species and breeding success (e.g. Piersma, 1987;

Piersma et al., 1993a; van der Zee et al., 2012) may also be affecting the macrobenthic communities and thus, the results.

Differences in shorebird community between low and high crab density areas

Results from this study clearly show that fiddler crabs have a strong effect on the spatial distribution of the shorebird community. The density of most species is drastically different between low and high crab density areas (a magnitude up to 20× in some species), with some species being more abundant in areas with low density of fiddler crabs, while others show the opposite pattern. Nevertheless, and overall, shorebird densities were higher in low crab density areas. In low crab density areas, the shorebird community is dominated by Red knot, Curlew sandpiper, Ringed plover and Sanderling. Moreover, the Little stint is almost exclusive to these areas. On the other hand, the shorebird community in high crab density areas is dominated by the Whimbrel, Common redshank, Common sandpiper and Sacred ibis. Additionally, the Common sandpiper is almost exclusive to areas with high densities of fiddler crabs.

Given that areas with high densities of fiddler crabs have lower richness and biomass of harvestable macroinvertebrates (see above), these areas are likely less attractive for most foraging shorebirds. However, fiddler crabs themselves are prey items of great importance for several shorebird species in the Bijagós. Previous studies have found that a high proportion of the diet in many species of shorebirds, including in the Ringed plover, Grey plover, Common redshank, Sacred ibis, Kentish plover, Curlew, Common sandpiper, Bar-tailed godwit, Sanderling, Rudy turnstone and Whimbrel, is composed by fiddler crabs (Zwarts, 1995; Lourenço et al. 2017). Some of these species have especially high proportions of fiddler crab in their diet and can be considered fiddler crab specialists in the Bijagós. These are the species that showed significantly higher densities in high crab density areas like the Whimbrel, the Common sandpiper, Common redshank, Sacred ibis and Curlew. The other species that feed on fiddler crabs but are not specialists either seem to show no preference in terms of foraging areas, like the Grey and Kentish plovers and the Bar-tailed godwit, or prefer low crab density areas, like the Ringed plover and Sanderling. This may be due to the fact that the other invertebrates relevant in their diet (Lourenço et al., 2017) are much scarcer in high crab density areas while crabs from the preferred size classes (0-1 cm, Zwarts, 1995), are present in both low and high crab density areas. Moreover, although these size classes have higher densities in high crab density areas, plovers are known to be mainly visual foragers that depend on sight to detect their prey, and the Sanderling and Bar-tailed godwit are mainly tactile foragers, that use their beaks to probe for prey (Zwarts et al., 1990; Lourenço et al., 2008). The presence of larger crabs that are not suitable prey items may increase the difficulty of the foraging activity.

Some of the studied birds are known to feed mainly on either polychaetes, such as the Dunlin (Lourenço et al., 2016), Curlew sandpiper (Puttick, 1978; Kalejta, 1993) White-fronted plover (Kalejta, 1993) and Little stint (Bengston & Svensson, 1968), or on bivalves, such as the Red knot (Lourenço et al., 2017) and Eurasian oystercatcher (Piersma et al., 1993b). All these species were found to have lower densities in high crab density areas, where their main food source is less abundant, except for the Eurasian oystercatcher and White-fronted plover. For the Oystercatcher, factors not evaluated may be influencing the results, like intraspecific interactions, that has been found to be an important factor determining the spatial distribution of this species (Ens & Goss-Custard, 1984). In the case of the White-fronted plover, the preference for Nereidae polychaetes, available in both crab density areas may explain the lack of significant differences. Moreover, all the above-mentioned shorebird species are known to

be mainly tactile foragers that devote a large proportion of time to random probing through which they find prey (Lourenço et al., 2017). The disturbance created by the larger and more abundant crabs in high crab density areas may prevent the birds from using their preferred foraging strategy.

The diet of the Common greenshank has been shown in previous studies to comprise mainly fish (Ntiamoa-Baidu et al., 1998), polychaetes and crabs (Kalejta, 1993). This wide variety of prey items may explain the non-significant differences found in the density of Common greenshank between low and high crab density areas. Moreover, we collected no data regarding the availability of small fish for waders and for Common greenshank the distribution of fish can be affecting the results. Also, this species was not very abundant in the study area and the low sample size may mask any possibly existing pattern of crab density preference.

Since fiddler crabs are generally distributed in large patches within the intertidal mudflat, their presence must have a strong effect on the spatial segregation and zoning of the shorebird species in the whole Adonga mudflats. This effect must be especially strong for some locally abundant species like the Whimbrel, Curlew sandpiper, Red knot, Ringed plover and Sanderling as shown by the marked differences in abundance in our study plots, but not very strong in some other abundant species like Grey plover and Bar-tailed godwit that did not exhibit significant differences.

Foraging behavior and diet of shorebirds in low and high crab density areas

We expected that shorebirds would be feeding more frequently on fiddler crabs in high crab density areas. However, except for Grey plover, no other species analyzed showed an increase in the consumption rate of fiddler crabs in high crab density areas, not even the highly specialized crab hunter Whimbrel. It is important to note that we measured the consumption rate as individual preys consumed per minute and not biomass consumed per minute. Due to the difficulty in approaching birds in the study area without disturbing them, the videos were recorded at a considerable distance and thus it was virtually impossible to accurately estimate the size of the prey consumed and estimate associated biomass. Since fiddler crabs are overall larger in high crab density areas it is likely that biomass intake is higher there, but without a biomass estimation we cannot say for sure. The only other differences in diet were registered for the consumption rate of Bivalvia/Gastropoda prey. Whimbrel ingested more bivalves and/or gastropods in low crab density areas and Grey plover ingesting less. Both these predators feed mainly on fiddler crabs but to a small extent, Whimbrel also preys upon bivalves and Grey plover upon polychaetes and gastropods (Zwarts, 1995; Lourenço et al., 2017). This may explain the increase in Bivalvia/Gastropoda prey consumption in low crab density areas by Whimbrel were the availability of crabs is lower, especially the preferred size classes (1-1.5 and 1.5-2 cm; Zwarts, 1995). For Grey plover the increase in Bivalvia/Gastropoda consumption in high crab density areas is contrary to the expected since these invertebrates are less abundant in these areas. Still, this data can be somehow biased as there was a high proportion of not identified prey items (also for Redshank).

We found no major differences in the foraging behavior of birds feeding in low and high crab density areas across all the species filmed. An exception was recorded for the parameter “pecking rate”, which increased in low crab density areas for all species except for Grey plover. This increase was not expected to occur in low crab density areas, but in high crab density areas, that hold a high availability of fiddler crabs. This increase is difficult to explain and further investigation on the matter may be needed to truly understand what may cause these differences. Moreover, the higher pecking rate does not seem to translate into a higher feeding success, as this parameter was not different between areas. It is important to note that all the four species included in this analysis are mainly visual foragers, although Whimbrel

and Redshank can sometimes use tactile cues to find prey (Lourenço et al., 2017). Thus, the lack of significant behavioral differences between areas can be explained by the low behavioural plasticity in these species. We also acknowledge that the relatively low number of videos recorded can also be shading potential differences, and an increase in sample size would be important to support these results.

Characterization of the fiddler crab populations in Adonga mudflats: a singular case?

Our results show that the fiddler crab population is female-biased in high crab density areas while the opposite was found for low crab density areas. The contrasting results obtained may be influenced by the low number of individuals sampled in low crab density areas since the sex of most crabs in these areas could not be determined due to their small size. Interestingly, the results obtained in high crab density areas do not concur with most previous studies performed in other habitats, where there was either a male bias in the sex-ratio of fiddler crab populations (e.g. Moruf & Ojetayo, 2017) or a balanced sex-ratio (e.g. Moruf & Lawal-Are, 2017). This shows that the fiddler crab populations of Adonga mudflats may be unique in this aspect. In terms of crab/burrow ratio, it has been well documented in previous studies that fiddler crabs dig burrows in excess, although the exact ratio varies between species and populations, even depending on some biotic and/or abiotic factors, like food supply (Genoni, 1991). Nevertheless, our results point for the lowest crab/burrow ratio previously described, meaning that the fiddler crabs in this area dig many burrows in excess (ca. 1 crab per 4 burrows), more than it would be expected.

Conclusions

This study presents strong evidence for the role of fiddler crab populations in shaping the structure of the remaining macroinvertebrate communities as well as the spatial distribution of foraging shorebirds. Impacts of fiddler crabs are probably driven by bioturbation resulting from their foraging activity which changes the sediment characteristics, in particular increasing the fine particle and organic matter content. These changes, along with the disturbance factor, are likely to be the promoters of changes in the benthic macroinvertebrate community, whose density and biomass were significantly lower in high crab density areas. Fiddler crab occurrence also affected the main predator of the macroinvertebrates, the shorebirds, whose distribution is affected by the distribution of their prey. Indeed, the shorebird community showed lower diversity in high crab density areas, while areas with low crab densities hold overall higher bird numbers. In particular, shorebird species that prey mainly on polychaetes, bivalves and gastropods seem to avoid areas densely occupied by fiddler crabs. In contrast, birds that prey mainly on fiddler crabs seemed to prefer high crab density areas. Although we found a clear effect of the fiddler crabs on the spatial distribution of foraging shorebirds, no behavioral differences were apparent in foraging birds between high and low crab density areas, which may also reflect the recorded lack of dietary differences between the two types of areas.

Results from our study are extremely relevant for the current knowledge on wintering shorebirds in the Bijagós archipelago. Fiddler crabs are largely widespread in the intertidal mudflats of the Bijagós archipelago and our data can be used to help predicting the most likely shorebird assemblages present in an area based on the presence of fiddler crabs. Although, in general, high crab density areas hold poorer and less abundant shorebird communities, there are many species that depend almost entirely on the crabs present in these areas to survive during the non-breeding period. These findings are critical from a conservation perspective, as the Bijagós archipelago is the second most important area for

wintering shorebirds in West Africa. Moreover, this is an ecosystem that has large extensions of fiddler crab, thus, the effect they have on the foraging shorebirds must be very strong, especially for locally abundant species that show clear segregation between the two crab density areas. Additionally, the fiddler crab patches seem to be relatively easy to map using satellite imagery (Belo, 2019) or even drones. Therefore, it is easy to include them on predictive models of shorebird distribution. It will be essential from now on to include the presence of fiddler crabs in these models as we now know it is a very powerful variable influencing the entire shorebird community.

In the future, it may be also important to use satellite imagery to understand how the populations of fiddler crab evolve, and if the crab patches are dynamic or close to static. This knowledge may be critical to explain changes in both macroinvertebrate and shorebird abundance and distribution.

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